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Migration/dispersal patterns of YOY bay anchovy *Anchoa mitchilli* in the Chesapeake Bay: Sr:Ca analysis on an ubiquitous species

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ABSTRACT

Bay anchovy *Anchoa mitchilli* is an ubiquitous, abundant pelagic species in the Chesapeake Bay, and does not exhibit discrete modes of habitat use related to different life-history stages. Here we test whether patterns in distributions of young-of-the-year (YOY) bay anchovy found in the upper Chesapeake Bay resulted from past dispersal. Individual chronologies of otolith strontium were constructed for 55 bay anchovy aged 43-103 d, collected at five Chesapeake Bay mainstem sites representing upper, middle, and lower regions of the Bay during September 1998. Analysis on these chronologies revealed the following:

1) Most YOY anchovy were estimated to have originated from the lower bay.
2) Those collected at 5 and 11psu sites exhibited the highest past dispersal rates, all in an up-estuary direction.
3) No significant net dispersal up- or down-estuary occurred for recruits captured at the polyhaline (>=18 psu) site.
4) Initiation of ingress to lower salinity waters (<15 psu) was estimated to occur near time of metamorphosis at lengths >25 mm SL and 50 days of age.
5) Estimated maximum upstream dispersal rate during the first 50-100 days of life exceeded 50 mm (>1.5 body length) per second.

INTRODUCTION

Patterns of dispersal and migration are important determinant in recruitment success. However, for ubiquitous, abundant species such as sardine, anchovy, herring, walleye pollock, etc., it has been difficult to document how dispersal and recruitment are linked using traditional sampling/tagging approaches. Because they do not exhibit discrete modes of distribution in their habitat, differential mortality rate across areas might lead to the false conclusion of dispersal among areas. Thus to investigate migration pattern, we use a longitudinal record of ontogenetic migration for individual fish.

Bay anchovy *Anchoa mitchilli* is the most abundant fish (Houde and Zastrow 1991) in Chesapeake Bay. The largest estuary in the United States, the Bay has a well-defined salinity gradient from its head to its mouth throughout the year. Bay anchovy is a key forage species for several economically-important fishes (Hartman and Brandt 1995). They are euryhaline, and ubiquitous in their distribution within the Chesapeake Bay. They spawn at salinities >5 psu, primarily from mid-May through mid-August (Zastrow et al. 1991). Although maximum spawning occurs typically at salinities >15 psu (Rilling and Houde 1999a), young-of-the-year (YOY) recruits are in high abundance in samples collected in oligohaline waters (Dovel 1971). Spatial patterns in abundance of Chesapeake Bay anchovy eggs and subsequent distributions of larvae and juveniles suggest transport and/or migration from lower bay and offshore spawning areas to up-estuary nursery areas (Dovel 1971; MacGregor and Houde 1996). While this behavior was postulated to be important to recruitment, there are no direct measures to confirm up-estuary dispersal or dispersal rates during the larval or juvenile stages.

In this study, we applied electron microprobe analysis (EPMA) of otolith strontium to investigate estuarine dispersal patterns of larval and juvenile bay anchovy in Chesapeake Bay. For several estuarine fishes, otolith strontium is a useful tracer of ontogenetic and seasonal migrations (Secor et al. 1995; Campana 1999; Secor and Rooker 2000). The objectives of this study were: 1) to verify that otolith Sr levels were related to ambient salinity for bay anchovy; 2) to test the hypothesis that YOY anchovies in the upper bay originated in lower bay regions; and 3) to estimate rates and ontogenetic patterns of bay anchovy dispersal.

MATERIALS AND METHODS

Fish Collection

Samples were collected at five sites representing different salinity levels in the Chesapeake Bay mainstem during the week 7-14 September 1998. Salinities at sites were determined from CTD casts. Sites had the following salinity ranges: 0-5, 6-11, 12-17, 18-23, 24-29+ psu (Fig.1; Table 1). Because we were unable to ascertain depth at which YOY were collected, we recorded site salinity as the mean of surface and bottom salinities. YOY bay anchovy were collected in 20-min. oblique tows of an 18-m^2 mouth-opening midwater trawl with 6-mm mesh liner in the codend. Sampled anchovy were preserved in 95% ethanol. For each site, five YOY anchovy from two size classes, 22-35 and 35-45 mm were chosen for analysis. At the 5 psu site, five additional YOY were examined. To test whether larvae and juveniles show different responses of otolith Sr level to salinity, we analyzed additional samples of otoliths from ten larvae (12 - 15 mm SL) collected in waters of 10, 20, and 25 psu based on Tucker trawl samples taken in July 1995 and 1997.

Otolith Microprobe Analysis

Otolith preparation and analytical methods for measuring molar weights of Sr and Ca followed those described by Secor et al. (1995). The minimum detection limits for Sr and the

Sr:Ca ratio in this analysis were 350 ppm and 0.32 x10^{-3}, respectively. In cases where Sr:Ca ratios were below this limit (1.8% of 1025 probed points), we used the value 0.32 x10^{-3} in statistical analyses.

Two types of EPMA were performed: marginal point and transect analyses. Marginal analysis included two or three discrete point measurements to evaluate the relationship between otolith Sr:Ca and ambient salinity. Transect analysis comprised a time series of point measurements beginning at the otolith core and ending at the peripheral edge of the postrostrum. Adjacent points were spaced at 30 µm intervals. To minimize the unknown effect of instrument drift, we blocked samples in a slide by site so that an otolith from each site was measured in turn. Using light microscopy, distances from the core to each transect point were measured to the nearest 1 µm.

Otolith Microstructure

Ages based upon otolith daily increments were determined from randomly drawn subsamples of 15 YOY and five larvae. Five sagittal otoliths each were sub-sampled from three YOY size bins to ensure that ages were estimated for all length classes in the sample. Otolith daily increments were counted independently three times under a compound light microscope at 150-300 x magnification. Age (= increment counts plus two; Zastrow et al. 1991) at each probe measurement was estimated based upon a regression of age on otolith maximum radius (OR). The relationship between standard length (SL) and OR was described by linear regression.

Dispersal Rate

Past dispersal rates of YOY were calculated based upon EPMA analysis and monthly Bay monitoring data:

1) **Mean Sr:Ca values were computed for each YOY corresponding to its first 20 days of life;**
2) **The mean Sr:Ca value was converted to salinity based upon a regression of ambient salinity on otolith Sr:Ca;**
3) **Depth-averaged salinity contour maps of the Chesapeake Bay's mainstem were constructed based upon monitoring data (Chesapeake Bay Program, Annapolis, MD, USA) for June and July 1998 using a kriging procedure (Surfer, Golden Software Inc., USA);**
4) **Isohalines (1 psu) were plotted, and where these crossed the longitudinal mid-axis of the Bay mainstem, potential sites of origin were plotted to the nearest 0.1 psu;**
5) **YOY were assigned to sites on either June or July monthly salinity maps based upon their hatch dates;**
6) **Dispersal distance was computed by summing mid-axis distances (km) across isohalines separating site of origin and collection site; and**
7) **Dispersal distances were divided by predicted age to estimate dispersal rates. In cases where salinity at the site of origin was >24 psu (n = 13), we designated the point of origin as the mouth of the Bay.**

Data Analysis

Inferential statistics were used to address the following questions:

1. **Are past dispersal rates related to site of collection?**
2. **Are dispersal rates of larval/YOY stage bay anchovy constant over their ontogeny?**

The first question was addressed based upon univariate analysis of variance (ANOVA) using the response variable Sr:Ca_{disp} which is the difference between the mean Sr:Ca measured for the first 20 days of life and the mean Sr:Ca measured for the last 2-8 days of life (three probe points each). The effect of site of collection on this index of dispersal was tested. Comparison of Sr:Ca_{disp} means among collection sites was conducted with a Tukey *post hoc* test.

The second question, relating to ontogenetic patterns of dispersal, was evaluated using repeated measures ANOVA (Chambers and Miller 1995). Statistical procedures utilized mixed model analysis (SAS8). Each transect of the probe points was divided into five age stanzas at

intervals of 15 days and mean Sr:Ca values for stanzas were computed in 28 YOY which were each >75 days of age. Age stanza were 15-29, 30-44, 45-59, 60-74, and 75-89 days. We tested the expected mean by fitting an unstructured covariance matrix (Littell et al. 1996). The covariance matrix did show declining covariance (correlation) as observations became increasingly separated in time. We use the unstructured covariance structure to test the following model

$$\text{Sr:Ca}_{1...5} = \text{Site} + \text{Age-class} + \text{Site} \times \text{Age-class}$$

where $\text{Sr:Ca}_{1...5}$ is the otolith transect time series of Sr:Ca values (Age-stanzas 1...5) for each chronology. The interaction term tested for ontogenetic differences in dispersal among collection sites. *Post-hoc* contrasts were directed at the question: At which age stanzas do up-estuary dispersals from polyhaline sites occur?

RESULTS

Estimated age of sampled larval and YOY anchovy (13.7 to 44.2 mm SL) ranged from 15 to 101 days after hatch. The daily growth rate, estimated from a linear model fit to size on age data ($r^2 = 0.96$), was 0.40 mm/d. Otolith radius was highly correlated with fish length (SL = 0.042OR+10.35; $r^2 = 0.99$) and age (Age = 0.103OR+15.33; $r^2 = 0.97$).

Marginal Point Analysis

Analysis of covariance detected no significant differences between larvae and YOY in the relationship: otolith marginal Sr:Ca and ambient salinity ($p = 0.9$). We observed no significant correlation between Sr:Ca and ambient temperature ($r^2 = 0.03$). For combined life history stages, marginal Sr:Ca was positively correlated with ambient salinity ($r^2 = 0.54$, $p < 0.001$; Fig.2). Despite high variance in this relationship, there were significant differences in mean Sr:Ca levels for YOY captured at sites with salinity <15 psu and those captured at sites >15 psu (ANOVA; $p < 0.001$). The data supported a criterion level of Sr:Ca = 0.8×10^{-3}, which separated regions <12 psu from regions ≥ 18 psu.

Transect Analysis

Larger size-class YOY fish for 21 and 28-psu collection sites, showed levels of Sr:Ca greater than 0.8×10^{-3} (polyhaline habitat use) throughout their lives (Fig. 3a,b). For YOY collected at 5-15 psu, transect Sr:Ca values initially corresponded to polyhaline habitat use, but in most cases decreased to levels lower than 0.8×10^{-3} at ages >50 days after hatch, or ≥25 mm SL (based upon regression) (Fig. 3c-f). Smaller (<35 mm SL) YOY showed the same trends. For YOY collected at polyhaline collection sites, Sr:Ca ratios indicated mesohaline or polyhaline habitat use throughout life; for YOY collected at 5 and 11 psu sites, Sr:Ca declined, indicating early polyhaline habitat use followed by gradual dispersal to oligohaline habitats.

Estimated dispersal of individual fish from June or July to September, 1998 at each collection site are shown in Fig. 4, and apparent upbay dispersal rates differed (Table 2). The rate was higher for the upper bay site than for lower bay sites. For YOY collected at the 5 psu site, maximum dispersal rate was estimated to be 5.6 km d^{-1} (65 mm s^{-1}) with the mean of 3.4 km d^{-1} (40 mm s^{-1}). Past dispersal rates were similar for YOY collected at 11 psu. At 15 psu, maximum rate was 3.4 km d^{-1} and at polyhaline collection sites, rates ranged from 0.4 - 0.8 km d^{-1} (4 - 9 mm s^{-1}), and offered little evidence of directional dispersal. Lifetime differences in Sr:Ca (Sr:Ca_{disp}) were significantly affected by site of collection (ANOVA; $p = 0.005$). Multiple comparisons of means indicated that YOY collected at 5 psu, 11 psu, and 15 psu had significantly higher lifetime dispersal rates than those collected at 28 psu (Fig. 5b). All other pair-wise comparisons were nonsignficant. Site of collection did not significantly influence Sr:Ca measures near the otolith core (Fig. 5a), suggesting that all analyzed larvae originated from a similar range of salinity, i.e. >15 psu.

<u>Ontogenetic trend</u>

Ontogenetic trends in repeated measures of Sr:Ca were significant and differed according to collection sites (Site x Age-class, $p < 0.001$). Because previous observations and analysis indicated that Sr:Ca values early in life did not differ among destination sites, we compared age-specific Sr:Ca between YOY anchovy collected at the combined polyhaline sites (21-28 psu) with those collected at 5, 11, and 15 psu. For age classes 15-29 and 30-44 days after hatch, there were no significant differences among sites ($p > 0.1$). However, Sr:Ca levels for YOY collected at 5 and 11 psu departed signficantly from levels of the polyhaline group at age class 45-59 days ($p < 0.05$; Fig.6). These differences were maintained for older age-classes. Differences in Sr:Ca levels for YOY collected at 15 psu were significant initially for age class 60-74 days ($p < 0.04$) and this difference was maintained for the 75-89 days age class.

DISCUSSION

Application of otolith strontium to an ubiquitous species in Chesapeake Bay has revealed individual migration/dispersal pattern to a specific region along the Bay's salinity gradient. Ontogenetic patterns in Sr:Ca in otoliths and analyses of variance in Sr:Ca vectors provided evidence for past up-estuary dispersal by Chesapeake Bay YOY bay anchovy collected at 5 and 11 psu sites. Sr:Ca ratios during the first 20 days of life did not differ among destination sites and were $> 0.8 \times 10^{-3}$, suggesting that most YOY anchovy in 1998 had originated from either polyhaline or mesohaline spawning sites. This result is in agreement with Rilling and Houde (1999a; 1999b) who observed that in 1993 eggs and larvae were most abundant in the middle and lower Chesapeake Bay, and also with observations in more recent surveys conducted from 1995-1999 (NSF TIES Program). After the larval stage, otolith Sr:Ca transects showed that some, but not all, YOY dispersed to oligohaline regions. Thus, EPMA analysis of otolith Sr supported the hypothesis of size- or age-specific directed dispersal by early-stage bay anchovy. But, in contrast to previous studies which proposed that up-estuary displacements occurred during the larval stage (Dovel 1971; Loos and Perry 1991), we observed up-estuary dispersal only during the early juvenile, or possible late-larval, stage (ca. > 50 days).

Individuals collected at 5-11 psu initiated detectable up-estuary dispersals between ages of 45-59 days at ca. ≥ 25 mm SL. This timing coincides with the larval transformation and early juvenile period, near the time of metamorphosis (Houde and Zastrow 1991). In coastal demersal species like Japanese flounder *Paralicthyth olivaceus*, plaice *Pleuronectes platessa*, and red sea bream *Pagrus major*, habitat shifts which correspond to juvenile metamorphosis are well documented (Minami, 1982; Rijnsdorp et al. 1985; Tanaka, 1985). In these species, shifts in habitat at metamorphosis are conspicuous due to marked changes in biological and habitat attributes associated with the niche shift. Subtler ontogenetic habitat shifts by estuarine fishes may occur across salinity regimes, but these have been difficult to document and investigate using traditional sampling and tagging approaches. This is especially true for pelagic species such as bay anchovy that are ubiquitous, abundant, and do not exhibit discrete modes of habitat use related to different life-history stages.

Results of EPMA depend upon the assumption that Sr:Ca is a scalar of salinity (Secor and Rooker 2000). Regression of marginal otolith Sr:Ca on ambient salinity supported this assumption. Still, the regression showed considerable variance, particularly at 15 psu. Ambient salinity (i.e. salinity at capture) may be an imprecise measure of salinities. But the regression was sufficiently robust to separate anchovy collected from oligohaline and polyhaline habitats and thereby supports Sr:Ca as an index of habitat use by salinity zone and $Sr{:}Ca_{disp}$ as an overall vector of dispersal.

Estimates of over-the-ground dispersal rates (Table 2) were uncertain given the imprecise prediction of salinity from Sr:Ca (inverse regression to that shown in Fig. 2). Here, we must assume that estimates of salinity based upon Sr:Ca (albeit imprecise) are unbiased, but sample size is relatively low and probability of bias due to sampling error is significant. A second

important source of error is uncertainty in assigning place of origin as a consequence of anchovy inhabiting variable depths with potentially differing salinities. Because distributions of fish in the water column were combined for our samples, we used the mean salinity between surface and bottom in our analyses. Despite uncertainties related to prediction of place of origin, we have presented dispersal rates as coarse estimates, primarily to demonstrate how EPMA may be used to obtain dispersal rates.

Based upon the mean size at which oligohaline-destined YOY anchovy began to disperse (SL = 35 mm), maximum dispersal rate was ca. two body lengths per second. Blaxter and Hunter (1982) reported that cruising speeds in juvenile clupeoid fishes ranged from 1- 5 body lengths per second. Juveniles also could use selective tidal stream transport to accomplish up-estuary dispersal (Weinstein et al., 1980; Tanaka, 1985). Thus, it is probable that YOY anchovy are capable of directed migrations at our estimated dispersal rates.

While transect analysis of otolith Sr:Ca demonstrated up-estuary dispersal by bay anchovy, it remains unknown how, or if, this behavior is particularly beneficial to growth and survival by migrants. Dovel (1971) postulated that the zone of oligohaline water provides improved nursery conditions for estuarine fish larvae and juveniles. The maximum turbidity front (Schubel, 1968) occurs within the oligohaline zone and may concentrate zooplankton prey. In addition, the scyphomedusan *Chrysaora quinquecirrha,* an important predator on anchovy larvae (Purcell et al. 1994), does not survive in freshwater-oligohaline regions of Chesapeake Bay (Cargo and Schultz, 1966).

We showed that otolith Sr:Ca ratios can be used to identify oligohaline habitat use by YOY. In the future, the critical zone hypothesis - i.e. higher rates of recruitment occur from individuals that utilized oligohaline regions as nursery habitat - could be tested by hindcasting YOY habitat use from adult otoliths. Year-to-year variability in patterns of distributions of recruits is evident and annual variability in recruitment levels could be related to upbay dispersal rates and patterns. The EPMA approach, combined with analysis of stage-specific abundances, holds promise to explain how bay anchovy and other species disperse in estuaries during early life.

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Table 1. Collection sites and samples of young-of-the-year (YOY) Chesapeake Bay bay anchovy used for EPMA analysis of otolith Sr:Ca. Collections were made during September 1998. Site indicates designated salinity (mean of surface and bottom salinity levels).

Site	Location		Salinity (psu)			Temperature (C°)		No. YOY Analyzed	
(Region)	Lat.	Long.	Surface	Bottom	Mean	Surface	Bottom	Large	Small
5 psu (oligohaline)	39.21N	76.10W	5.0	6.0	5.5	26.2	26.1	10	5
11 psu (mesohaline)	39.10N	76.18W	9.9	11.8	10.9	25.8	25.8	5	5
15 psu (mesohaline)	38.20N	76.20W	14.4	15.8	15.1	24.9	25.2	5	5
21 psu (polyhaline)	37.30N	76.07W	19.6	21.4	20.5	24.1	24.8	5	5
28 psu (polyhaline)	37.00N	76.03W	28.0	28.8	28.4	22.8	22.8	5	5

Table 2. Upbay dispersal rates (km d^{-1}) predicted for Chesapeake Bay YOY bay anchovy based upon life-history transect measures of Sr:Ca.

Site	Mean ± S.D.	Maximum	Minimum
5 psu	3.4 ± 1.4	5.6	1.2
11 psu	3.4 ± 1.2	5.1	2.2
15 psu	2.3 ± 1.0	3.4	0.4
21 psu	0.8 ± 0.3	1.2	0.3
28 psu	0.4 ± 0.2	0.5	0.1

Figures

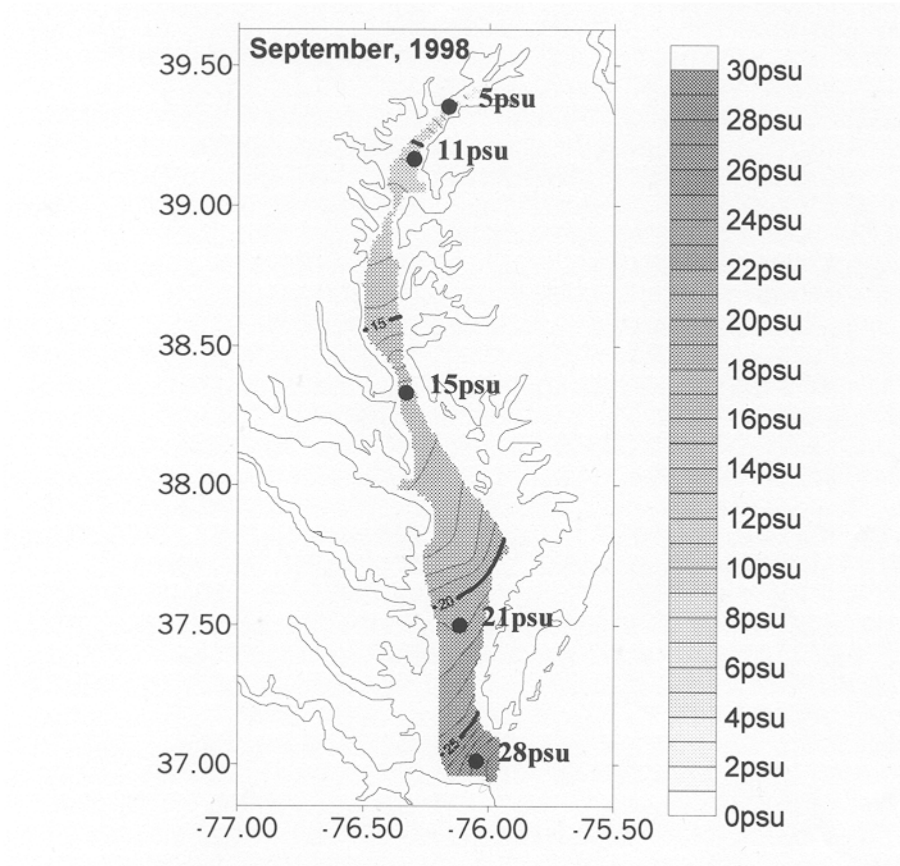

Figure 1. Salinity isopleths (1 psu) for Chesapeake Bay in September 1998 during the period that analyzed young-of-the-year bay anchovy were collected.

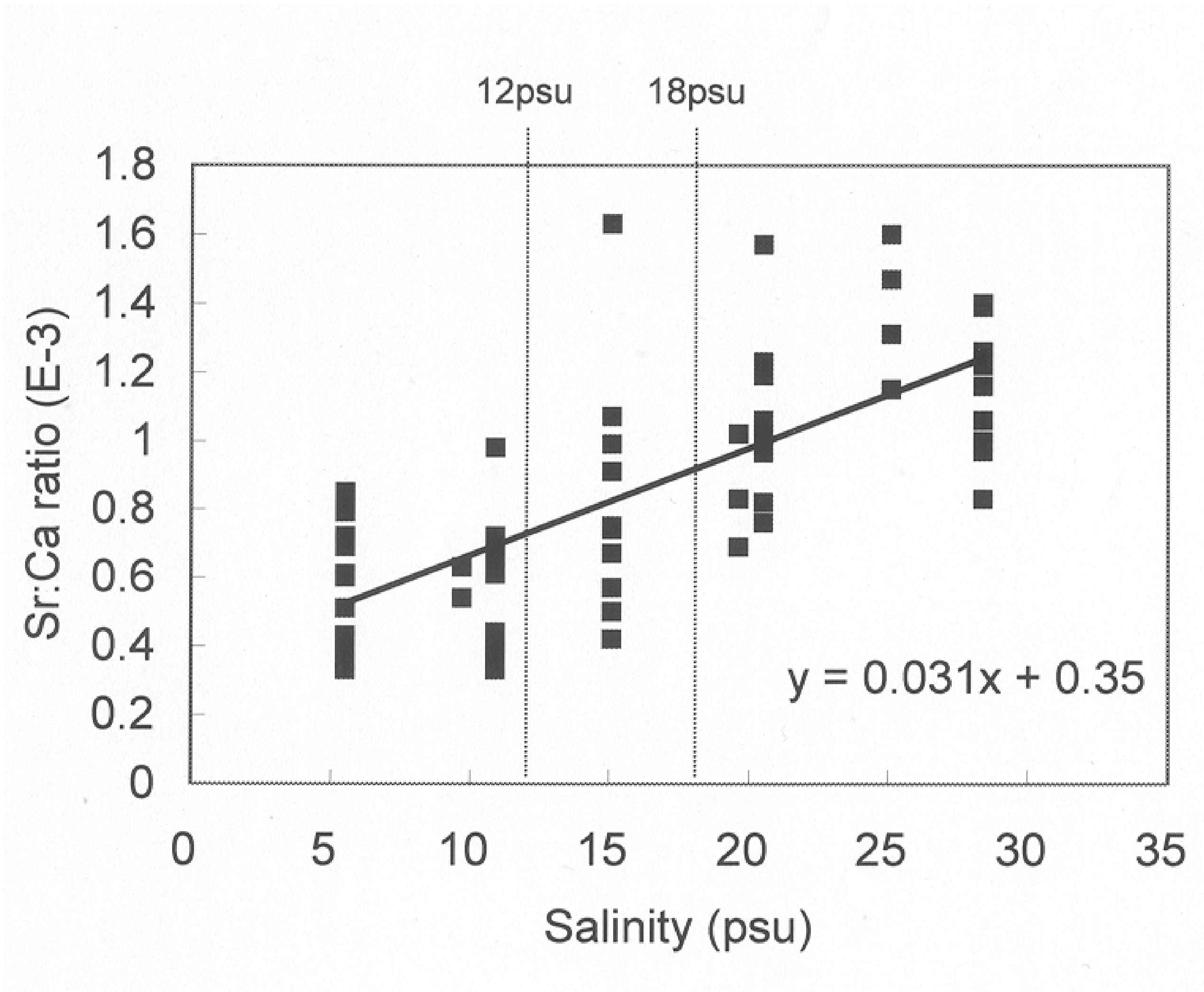

Figure 2. Regression of marginal Sr:Ca on ambient salinity for larvae and young-of-the-year Chesapeake Bay bay anchovy collected in 1995-1998.

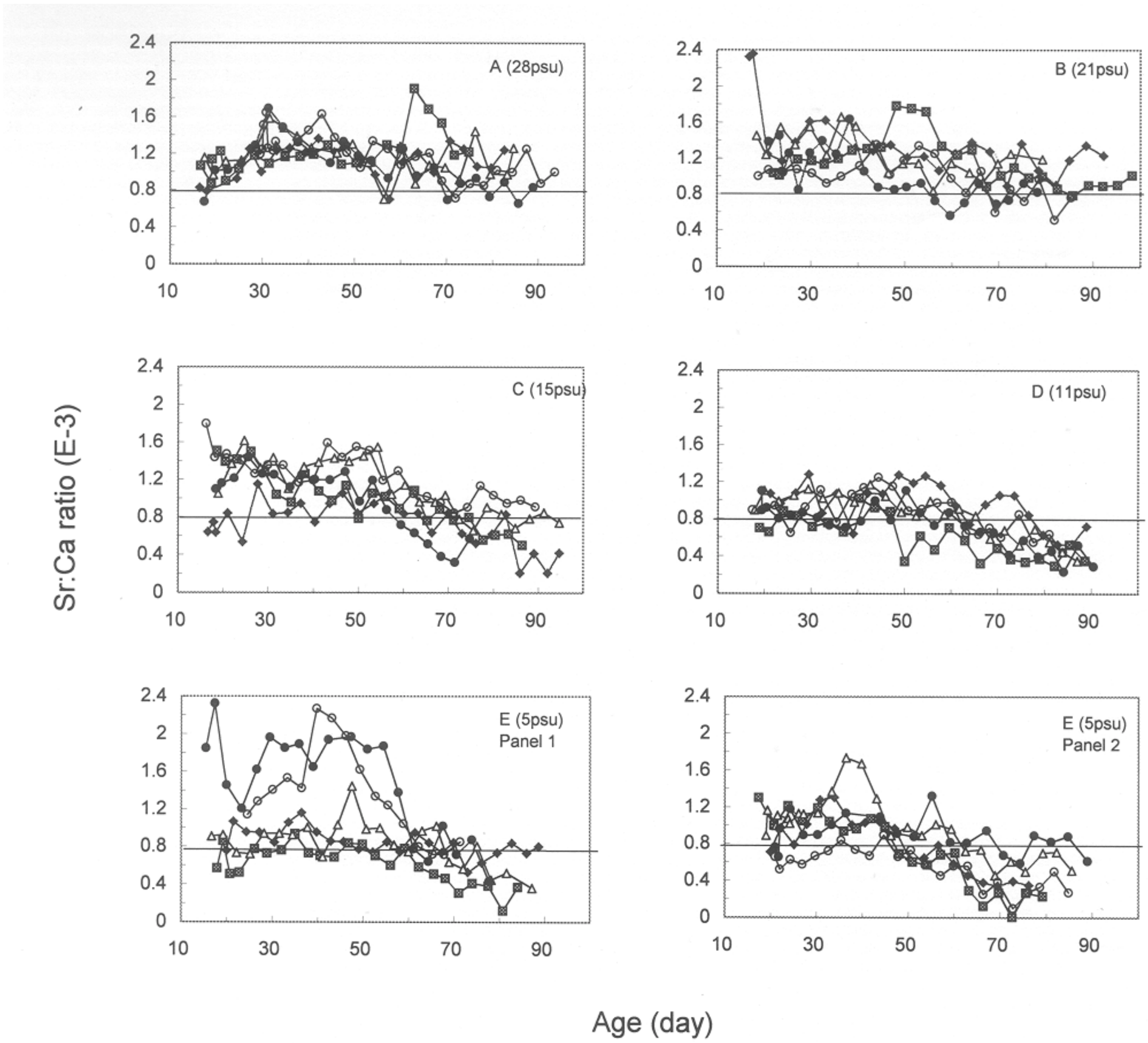

Figure 3. Sr:Ca transects on otoliths of large (≥35 mm SL) young-of-the-year Chesapeake Bay bay anchovy collected in 1998. Each line indicates a criterion level of Sr:Ca = 0.8×10^{-3}, which separated regions <12 psu from regions ≥ 18 psu.

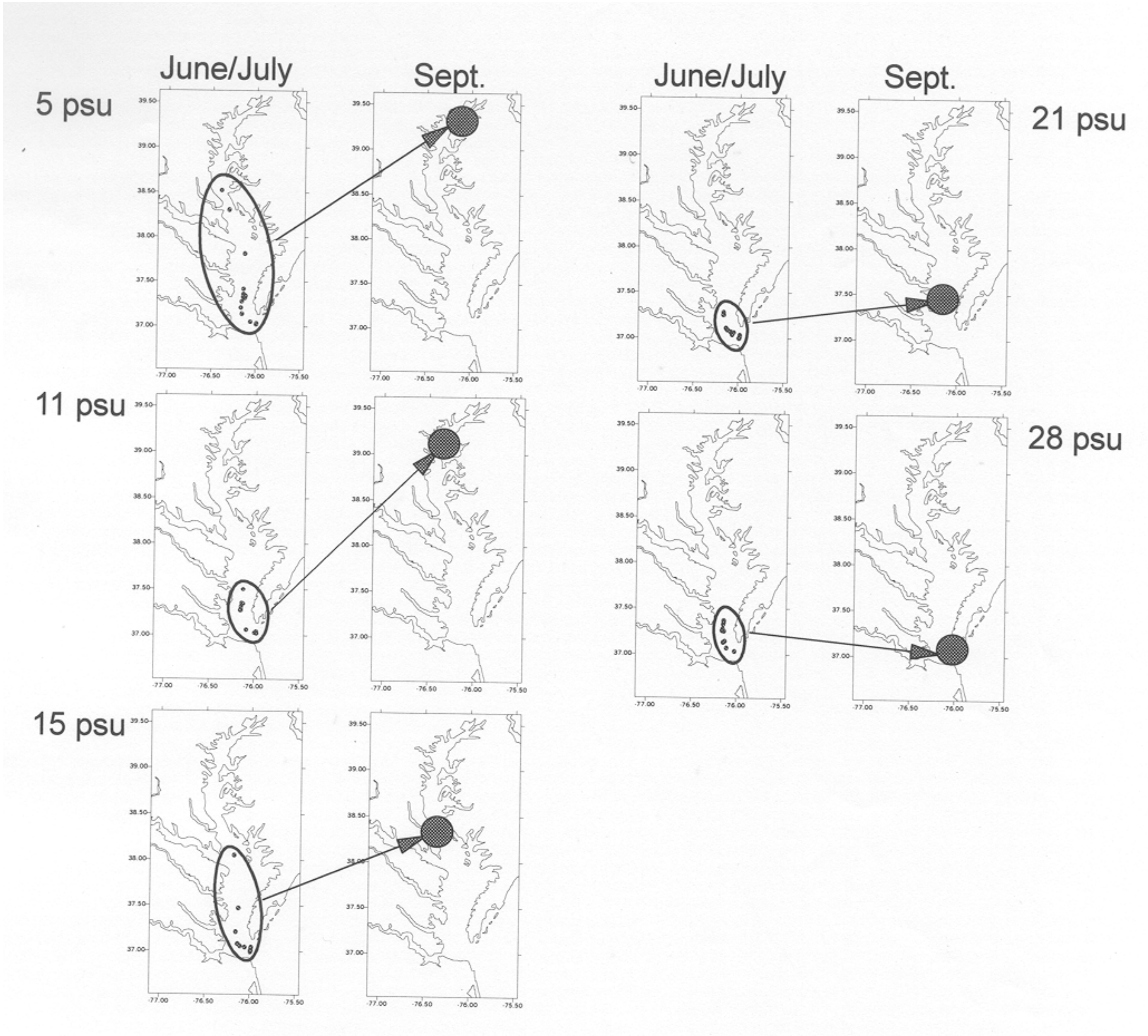

Figure 4. Estimated migration/dispersal of YOY bay anchovy in 1998, based upon the analysis of otolith Sr:Ca ratio. Figures represent the site salinity at capture. Dots on the June/July maps represent each estimated point corresponding to the first 20 days of life, and closed circles on the September maps represent the site at capture.

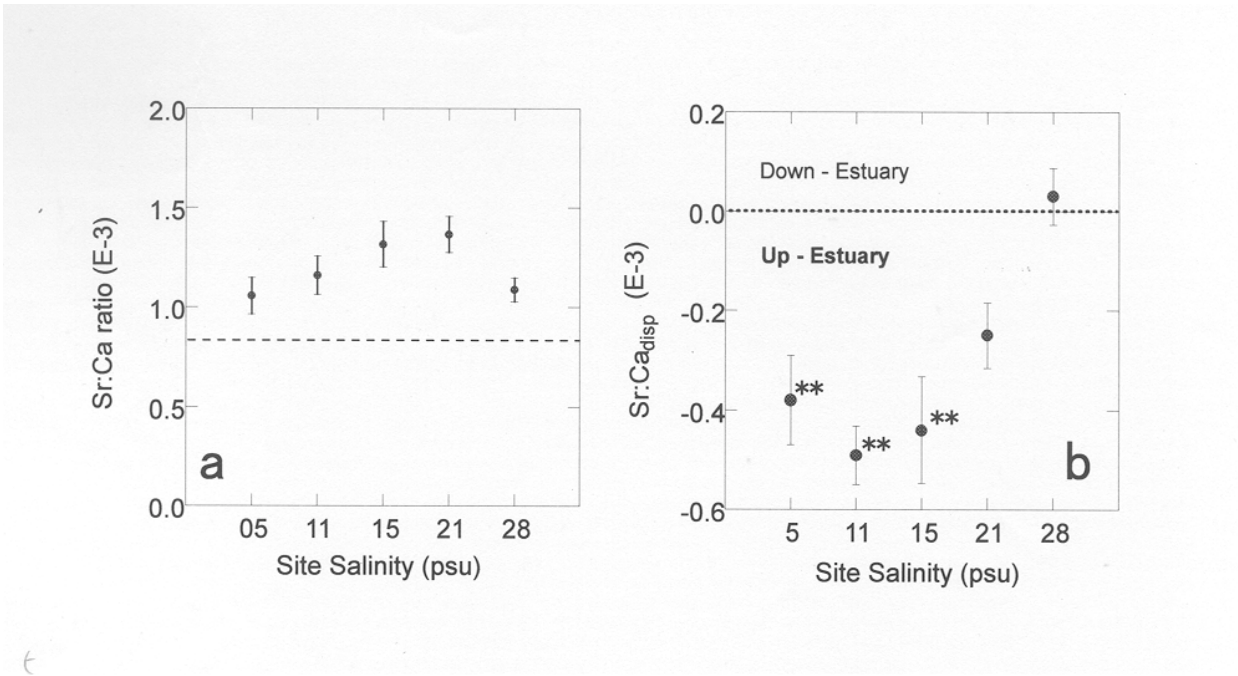

Figure 5. (a) Mean early (< ca. 20 days) larval Sr:Ca levels among collection sites for young-of-the-year Chesapeake Bay bay anchovy collected in 1998. (b) Mean dispersal vectors, Sr:Ca$_{disp}$, among collection sites for young-of-the-year Chesapeake Bay bay anchovy collected in 1998. Vertical bars represent ± 1 SE.

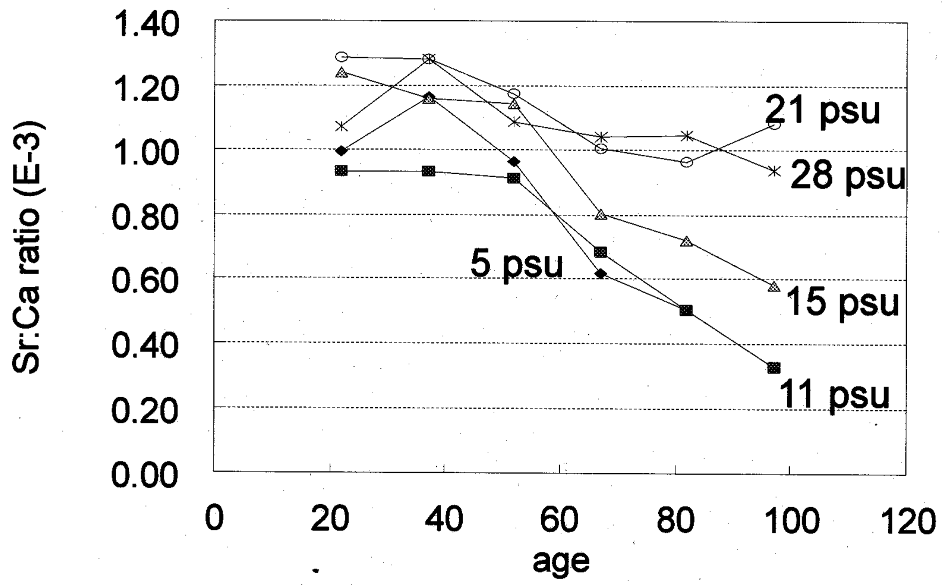

Figure 6. Change in mean Sr:Ca ratio of 5 site groups at each age stanza (15-29, 30-44, 45-59, 60-74, and 75-89 days). The 90-104 days age stanza was omitted from the statistical analysis because data were absent for the 5 psu site.